ORIGINAL ARTICLES.

Morphological Studies on the Echinoidea Holectypoida and their Allies.

X. ON *APATOPYGUS* GEN. NOV. AND THE AFFINITIES OF SOME RECENT NUCLEOLITOIDA AND CASSIDULOIDA.

By Herbert L. Hawkins, D.Sc., F.G.S., Professor of Geology, University College, Reading.

(PLATE VII.)

1. Introduction.

WHILE collating the plates in a recently acquired copy of the *Revision of the Echini* (A. Agassiz, 1872–4), I noticed with surprise a representation of complex ambulacral structure in "*Echinobrissus*" *recens* (pl. xiv *a*, figs. 3–4). A style of plate-grouping essentially similar to that in *Echinonëus* (tab. cit., figs. 7–8) is portrayed as affecting all the extra-petaloid parts of the five areas, and encroaching slightly on the distal parts of the petals. No reference to this unusual condition occurs in the text. As the proofs of my recent paper on ambulacral structures (Phil. Trans., B, vol. 209) were in my hands at the time, I was immediately impressed by the remarkable resemblance between "*E.*" *recens* and the Cretaceous *Trematopygus*—a correspondence by no means restricted to ambulacral plating, but involving all coronal features save the orientation of the peristome.

Within an hour of the discovery a letter was dispatched to Dr. H. L. Clark, of the Museum of Comparative Zoology, Cambridge, Mass., asking if he could confirm the presence of the structure indicated, and begging for any fragments of "*E.*" *recens* that could be spared. By return mail he sent me entire tests of three rare Echinoids, "*E.*" *recens* (to him an *Oligopodia*), *Oligopodia epigonus*, and *Rhynchopygus caribœarum*. He encouraged, nay commanded, me to work my will on the beautiful specimen of the first-named species, even if pulverization were the result, and placed but few restrictions on my treatment of the others. Some idea of the disinterested generosity shown can be conveyed on two counts. In the first place the specimens are recent forms on which Dr. Clark has been working lately, thereby "staking a claim" in them whose justice all would admit. But he handed them over to the tender mercies of a palæontologist who had not the temerity to ask for them! Secondly, Agassiz Museum possesses only four specimens of "*E.*" *recens* (one of which I was instructed to destroy), two of *O. epigonus* (the better of which, figured in the *Revision*, pl. xix *b*, figs. 4–6, is in my hands), and two of *R. caribœarum*.

The liberty and fraternity of science could scarcely have had more convincing exposition. In publicly expressing my gratitude to Dr. Clark and the Museum with which he is connected, I feel

constrained to hope that the spirit herein manifested may inspire an ever-growing *ecclesia* of individuals and institutions. A Museum whose aim is to acquire and store away a miserly hoard of rarities is in danger of becoming a mausoleum rather than a radiant centre of vitality in research; the individual who fails to welcome discoveries, even when they might have been his own, is no apt disciple, still less a true apostle, of the creed of science.

Of the three specimens sent for study "*O.*" *recens* is now in ruins (though even yet beautiful); *O. epigonus* has acquired a coloration unlike that secreted by any known Echinoid, and has unfortunately lost its apical system; while *R. caribœarum* has suffered removal of many of its radioles. It is my earnest hope that the following notes may atone in some measure for the damage done, and convey in the most acceptable form my thanks for the prompt and almost reckless generosity that enabled me to investigate material at once so precious and so interesting.

2. Apatopygus recens (Milne Edwards).

This species was introduced by Milne Edwards in 1836 (Cuvier, Regn. Anim. Zooph., pl. xiv, fig. 3), under the name *Nucleolites recens*. At that date *Nucleolites* was a broad generic term covering all Irregular Echinoids which have the periproct on the adapical surface; but in this particular case the close superficial similarity between *N. recens* and such fossil forms as *N. scutatus* made application of the name unusually appropriate. D'Orbigny in 1854 (Rev. Mag. Zool.) automatically replaced *Nucleolites* by the pre-Linnean *Echinobrissus*, but no reasoned attempt at better generic precision was made until 1889, when Duncan (Journ. Linn. Soc., vol. xxii) proposed *Oligopodia* as a subgenus, including the two recent species of "Nucleolitidæ" then known, *recens* and *epigonus*. In 1904 Hamann (Bronn's *Thierreichs*) raised *Oligopodia* to generic rank, and restricted it to *O. epigonus* (Martens), which thereby became the genotype. "*Echinobrissus*" *recens* was left in *Nucleolites* by Hamann, but Clark (1917, *Hawaiian and other Pacific Echini*, p. 107), believing *recens* and *epigonus* to be congeneric, and "quite different from typical *Nucleolites* of Lamarck", placed both under *Oligopodia*.

While concurring in Clark's opinion that both are incapable of bearing the name *Nucleolites*, I am fully convinced that they are so far from being congeneric that family, and indeed ordinal, distinctions separate them. The reasons for this belief are subjoined, but the systematic sequel can be indicated here. *Nucleolites epigonus* Martens is the lecto-genotype (Hamann, 1904) of *Oligopodia* Duncan, 1889. *Nucleolites recens* M. Edwards is certainly not a *Nucleolites* in the accepted sense of the term, and is even less akin to *O. epigonus*. A new generic name is thus necessary for *N. recens*, unless that species can be shown to belong to some other genus already diagnosed. The latter condition does not obtain, so far as I can determine,

so that I hereby establish the new genus *Apatopygus*,[1] whose genotype and only known species is *Nucleolites recens* Milne Edwards, 1836. A detailed diagnosis of the genus concludes this section of the paper.

The description of *Apatopygus recens* (sub *Echinobrissus*) given by A. Agassiz (*Revision*, pp. 556–7) is sufficiently full and in agreement with the specimen before me to serve with but little comment. The description of the peristome and its surroundings is accurate, but Agassiz' use of the term "phyllode" might prove misleading. There is no more trace of phyllodal qualities, whether of plating or pore-disposition, in the orad parts of the ambulacra than occurs in an ordinary Spatangid. The proximal pores are appreciably larger than the others, and tend to perforate their ambulacrals in the median line rather than near the adradial sutures; but the pores show less tendency towards triserial arrangement near the peristome than on the rest of the adoral surface, while the plating is almost perfectly simple and "Cidaroid" in the region where the pores increase in size. With regard to the interambulacral parts of the peristome-margin, there can be no doubt that Agassiz' remark that "no buccal bourrelet had been developed" is an under-statement. As far as such a condition is conceivable it may be said that "bourrelets" are positively absent—the proximal interambulacrals are exceptionally thin in their invaginated parts, resembling those of *Echinonëus* more than those of any other recent Echinoid with which I am acquainted, and exceeding them in delicacy. The quality expressed in the generic description (loc. cit., p. 556) "Floscelle rudimentary; no well-marked bourrelets" would, to my mind, be better abbreviated to the bare statement "no floscelle".

The nature of the ambulacral plating, which is roughly indicated in Agassiz' figures, but not mentioned in the text, seems to me to provide the most unusual and distinctive feature in *A. recens*. Analyses of one of the longest areas (I) and the shortest area (III) are here given (Plate VII, Figs. 1 and 2). As far as indications go, area II (which is almost midway between the extremes in point of length) resembles the latter more closely than the former. In all ambulacra, practically the entire extent of the adoral parts (excluding the peristomial portions above mentioned) display typically "Pyrinid" plating (see Hawkins, Phil. Trans., 1920), the demiplates often undergoing great reduction. In area I this condition ceases just below the ambitus, and the adapical part of the area is built of simple primaries, some of which (below the petals) may be almost half as high as broad. The petal consists of thirty plates in each column, perforated by dissimilar pore-pairs. In area III, Pyrinid structure persists up to, and even into, the petaloid region with characters indistinguishable from those present adorally.

[1] ἀπατάω, I deceive, and *-pygus*, normal suffix for genera of this group.

There are twenty-one or twenty-two plates in each column of the petal. Three or four of the distal plates of this region show incipient Pyrinid grouping, while a trifling imperfection of alternation affects both columns quite near the apex. (This last may well be but an individual irregularity.) The indications of structure given in Agassiz' figures are therefore confirmed (broadly speaking); but he represents Pyrinid plating as continuous to the petals in all five areas, while it certainly does not extend above the ambitus in areas I and V in the specimen before me, and seems not to reach the petals in II and IV.

The two features described above contain sufficient evidence for generic separation of *A. recens* from *O. epigonus* (Pl. VII, Figs. 3 and 4), although many others could be cited. In the latter species there is a perfectly definite floscelle, with expanded (though structurally simple) phyllodes and well-marked, typical interambulacral bourrelets. There is no trace of ambulacral complexity above the phyllodes; all ambulacrals between these and the petals are about as high as broad, and in consequence the number of podial pores is very small. All five petals are of the same length, and contain the same number of plates; while the petaloid pores are large and perfectly similar. The name *Oligopodia* is eminently appropriate for *epigonus*, but it would be grotesque to apply it to *recens*, where the number of ambulacral plates (and podia) is vastly in excess of expectation for so small a form. *O. epigonus* is a typical "Cassiduloid", and resembles *Rhynchopygus* and *Echinolampas* in ambulacral characters, as in many others. As Agassiz remarked, it is closely similar to the Cretaceous genus *Caratomus*. The affinities of *Apatopygus* will be discussed in the next section, but a diagnosis of the genus is now possible.

Apatopygus gen. nov., Hawkins, 1920.

Genotype and sole species, *Nucleolites recens*, M. Edwards, 1836.

Nucleolitoida, Nucleolitidæ. *Test* depressed, subquadrate, with greatest width behind the apex. *Ambitus* rounded, adapical surface rising to a low, almost median summit; adoral surface slightly tumid, strongly invaginated at the peristome. *Apical system* eccentric anteriorly, built of five small oculars and four genitals, of which the madreporic plate occupies the centre of the system, and just separates the posterior oculars. *Peristome* deeply invaginate, eccentric anteriorly, transversely elliptical, with thin marginal plates. *Periproct* longitudinally elliptical, situated in a deep sulcus to which it forms the apicad wall, about midway between the apex and the posterior margin of the test. Anus surrounded by a many-plated membrane, the largest plates being posterior and external. *Interambulacra* wide, built of fairly low plates bent near the median line of each column. Proximal orad interambulacrals large, single, and very thin. Tubercles large for a Nucleolitoid, scrobiculate, imperforate; arranged in quincunx on apicad and orad plates. *Ambulacra*

petaloid, narrow, widest at the ambitus. Posterior petals longer than anterior; that of area III the shortest. Petaloid pores dissimilar, outer pores elliptical and larger than the inner, round, pores. Extra-petaloid pores single and small, three or four in the peristomial invagination being slightly larger than the rest, but not attaining the size of the outer petaloid pores. Pore-series irregularly uniserial (with tendencies to triserial arrangement below the ambitus), convergent adorally. Proximal orad plates primaries (biporous ambulacrals present) within invaginated parts. Thence to ambitus typical "Pyrinid" plating, most intense (in part Discoidiid) in areas I and V. Similar plating continued above the ambitus into distal part of petal in area III, ? almost to petals in II and IV, but not reaching above ambitus in I and V. In areas last-named supra-ambital, non-petaloid plates are relatively high. Petals (except in III) uniformly Cidaroid in plating.

Recent: New Zealand and ? Madagascar.

3. The Affinities of *Apatopygus*.

The entire facies of the test of *Apatopygus* agrees very closely with that of *Nucleolites*, and is superficially almost identical with that of *Trematopygus*. The large size of the peristome, and the marked disparity in length of the petals are obvious features that distinguish it from the former, while the directly transverse elongation of the peristome runs counter to the diagnostic character of the latter. The ambulacral structure, with which this paper is mainly concerned, clearly separates *Apatopygus* from *Nucleolites*, and approximates it to *Trematopygus*. It is needless to argue further the close relationship connecting all three genera. To my mind the original contention that "*Nucleolites*" *recens* is a latter-day survivor of the essentially Mesozoic Nucleolitoida is perfectly justified.

In respect of ambulacral structure, it is possible to recognize four types in the Nucleolitidæ (*sens. str.*), each of which can be ascribed to a more or less defined place in stratigraphical history. The Lower Oolitic type (e.g. "*Nucleolites*" *quadratus*, see Phil. Trans., vol. 209, pl. lxviii, fig. 2) had well-marked, congested petals, and strictly limited phyllodes containing many occluded plates. The Upper Oolitic type (e.g. *Nucleolites scutatus*, loc. cit., pl. lxviii, fig. 3) had less-restricted, little-congested petals, and ill-defined hypophyllodes in which occluded plates are rare, but demi-plates may occur. The Cretaceous type (*Trematopygus*, loc. cit., pl. lxviii, fig. 4) had long, many-plated, but feebly expanded petals, and a strangely diffuse, vestigial kind of hypophyllode, in which Pyrinid plating covers much of the adoral extent of the ambulacra, being least extensive in areas I and V. The fourth type is *Apatopygus*, with long but uncongested petals, and an exaggerated state of diffusion in the "hypophyllode", which shows features normal to *Trematopygus* developed to a far greater extent. The four types surely illustrate a morphogenetic sequence. While petal-characters

appear to oscillate (save perhaps for steady reduction in the expansion of the petals), phyllode-development seems to show progressive (or, perhaps, regressive) modification. The plate-complexity that was concentrated into the true phyllodes of the older Nucleolitids (such as *Galeropygus* and "*Nucleolites*" *quadratus*) spread gradually away from the peristomial region until in area III of *Apatopygus* it involves the greater part of the area in triad-grouping. As far as phyllode-production is concerned, the change was catagenetic, but in respect of the complexity of the whole ambulacrum it was clearly anagenetic.

The sequence of ambulacral morphogenesis indicated above was carried out in a series of forms whose general evolution has been relatively static. Save for its ambulacral plating, *Apatopygus* would not have been out of place on a Middle Jurassic beach. Another line of descent from the *Galeropygus–Nucleolites* stock led in quite an opposite direction, and produced the *Clypeus–Pygurus* series with increasingly complex and limited phyllodes. That essentially Mesozoic group showed far more diversity in form, size, and detail than the conservative Nucleolitidæ, and paid the penalty of over-exuberance by extinction in the Cretaceous period. The two Nucleolitoid series thus provide clear illustration of the principles of evolution already familiar in many phyla. In comparison with Brachiopoda, *Apatopygus* may be said to bear a similar relation to *Galeropygus* to that borne by *Lingula* to *Lingulella*; while *Pygurus* would agree more with *Spirifer*. The persistent *Nautilus* and the extinct "*Ammonites*" have comparable histories.

The ambulacra of *Apatopygus* invite comparison with those of the Echinonëidæ. Save for the presence of petals and "biporous" orad ambulacrals, *A. recens* has typical Pyrinid ambulacral plating, almost perfect as far as it extends. In area I (Pl. VII, Fig. 1) there occur three Discoidiid triad-groups (similar plates appear in *Trematopygus*), so that the correspondence with Holectypoid structures is emphasized. It seems quite inconceivable that any phyletic link can connect *Apatopygus* with *Pyrina* or any other late Holectypoid; so that the appearance of Pyrinid plating in the recent form must be ascribed to parallel development.

If orthogenesis supplies an explanation of this coincidence, the separable qualities of the components of "individuals" is strikingly illustrated. The ambulacra of *Apatopygus* have come to conform to the Holectypoid standard in essentials (albeit by a non-Holectypoid route); while other coronal structures have followed quite different lines of development. Further, the appearance of Pyrinid plating in the last of the Nucleolitoida seems to give support to the belief that that stock branched from the Holectypoid series (though early) rather than arose independently. That extensive triad-grouping or combination after this pattern appeared in Lower Cretaceous times in the Echinina, Echinonëidæ, Lanieriidæ, and Nucleolitidæ, is a coincidence explicable only on the assumption

that morphogenesis may be not merely parallel in otherwise divergent stocks but proceeds at the same rate. Hence come "modes" or "fashions" prevalent in ultimately homogenetic series—sources of convenience to the stratigrapher and confusion to the systematist.

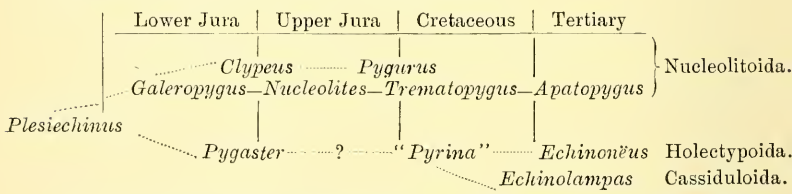
4. The Affinities of *Echinolampas*.

H. L. Clark (*Hawaiian and other Pacific Echini*, p. 143), commenting on my suggestion that the "Nucleolitidæ" (i.e. the Cassiduloidea of Sladen and Asternata of Gregory) may be diphyletic, states that "the recent species seem to form a very homogeneous group"; but he admits that "a more natural grouping in accordance with some of [my] suggestions" may prove possible. The earlier sections of this paper seem to me to show that *Apatopygus*, at least, is a very distinct type from the *Oligopodia–Rhynchopygus–Echinolampas* series of recent Cassiduloids. *Apatopygus* has definitely dissimilar petaloid pores—those of the Cassiduloida are similar and normally conjugate. I have no knowledge of any other living genus that can be associated with *Apatopygus* in the Nucleolitoida, and so agree with Clark as to the apparent homogeneity of his Nucleolitidæ with this single exception.

In several of the papers in this series, and especially in my recent memoir on ambulacra (Phil. Trans.), I have argued that the *Echinolampas*-series (which I call Cassiduloida *sens. str.*) are sequentially related to the early Echinonëidæ much as the Clypeastroida are to the Discoidiidæ. In the almost complete absence of knowledge of post-larval changes in recent Echinoids (zoologists, please note!), my arguments have necessarily been somewhat hypothetical or based on unverified assumptions. But in the section of Agassiz' Revision "On the young stages of Echini" (Part IV), p. 741, and in the plate (xvi) illustrative of the particular paragraph, something approaching ontogenetic proof of my contention appears. Agassiz says: "The development of *Echinolampas* has thrown unexpected light upon the affinities of the toothless Galerites and of the Cassidulidæ. It shows conclusively that *Echinonëus* is only a permanent embryonic stage of *Echinolampas*, thus becoming allied to the Cassidulidæ, and that it has nothing in common with the Galerites as I would limit them, confining them entirely to the group provided with teeth." These sentences were written long before Agassiz was able to record the presence of a vestigial lantern in young *Echinonëus*—in the light of that discovery the genus has almost everything "in common with the" Holectypoida. Study of Agassiz' drawings (pl. xvi, figs. 1–3) shows that *Echinolampas depressa*, when 4 mm. in diameter, is more like a *Conulus* or "*Globator*" than an *Echinonëus* in general facies, but has the tuberculation of a *Discoidea*. At a later stage, 12·7 mm. in diameter (tab. cit., figs. 8–10, here partly adapted, Pl. VII, Fig. 5), the test takes on a more depressed and elongate form, and the

tuberculation becomes amplified in the hour-glass pattern characteristic of *Conulus*. (In *E. sternopetala* Ag. & Clark, "*Conulus*-tuberculation" seems persistent even in the adult.) It is in the ambulacra, however, that the young *Echinolampas* exhibits the most remarkable qualities. Agassiz says of these (l.c., p. 742), "each plate . . . carries a single primary tubercle . . . The pores are arranged . . . three or four for each plate." His enlarged drawings (here Pl. VII, Fig. 5) show that "each plate" is really a triad-group. No indication appears as to the relations of the components of the groups, but that they are not all primaries seems probable from the nature of the perradial suture. In view of Agassiz' previously quoted remark, it is reasonable to assume that the triad-groups are Pyrinid in character, like those of *Echinonëus*. Such triadic structure is persistent in *Amblypygus* (otherwise very nearly akin to *Echinolampas*), but it is *not* retained in adults of *Echinolampas* itself. Its presence in early ontogeny must surely be vestigial. In consequence the descent of the *Echinolampas*-stock from an Echinonëid (or late Holectypoid) ancestry is a conception that is now so far established that it is for those who disagree to disprove it. Stratigraphy, morphology, and now ontogeny, all point to its truth.

The ambulacral history of the Nucleolitoida and Cassiduloida (assuming the above conclusions to be accurate) shows a strange course of morphogeny. The phyletic relations of the groups, as they appear to me, can be indicated thus :—



The Nucleolitoida early acquired elaborate phyllodes, retaining simplicity in the rest of their ambulacra. During the Mesozoic era their phyllodes underwent gradual decentralization, until triad-grouping affected a large part of the areas. This tendency culminates in *Apatopygus*. On the other hand, the Holectypoida failed to develop phyllodes, but progressively spread triad-grouping over their ambulacra (e.g. "*Pyrina*"). In the Tertiary era, simplification of plating, coupled with production of well-defined phyllodes (perhaps foreshadowed in *Conulus*), characterized the Cassiduloida. The two independent trends separated rapidly in the Lower Jurassic, and then slowly converged until, in the Cretaceous, they were almost coincident. Modern Cassiduloida have reached a stage analogous with that of the precocious Clypeidæ of the Nucleolitoida. But *Apatopygus* and *Echinonëus* remain as superannuated survivors, the last of their respective orders, wearing to-day the ambulacral fashions of the Cretaceous period.

EXPLANATION OF PLATE VII.

FIG. 1.—Analysis of ambulacrum I of *Apatopygus recens*, showing Pyrinid and Discoidiid plating below the ambitus, and dissimilarity of the petaloid pores. × c. 4.

FIG. 2.—Ambulacrum III of the same specimen, similarly enlarged. Pyrinid plating extends into the distal part of the petal.

FIG. 3.—Similar analysis of ambulacrum I of *Oligopodia epigonus*. An extremely simple phyllode is succeeded by "Bothriocidaroid' plates to the petal, which shows similar pores. This is a perfectly typical Cassiduloid ambulacrum, its phyllodal simplicity being probably due to the smallness of the species. × c. 6.

FIG. 4.—Ambulacrum III of the same specimen, similarly enlarged. Both areas have exactly comparable structure, and petals of precisely the same length.

(In these four figures the ambitus is indicated by small dashes.)

FIG. 5.—Part of corona of *Echinolampas depressa* at 12·7 mm. diameter. (Modified from A Agassiz, Revision, pl. xvi, fig. 11.) The interambulacral tuberculation is roughly like that of *Conulus*, but shows greater primitiveness in the scrobicular rings of granules. The ambulacral plates are grouped (or perhaps combined) into triads. The probable course of the sutures separating the individual plates is suggested by dotted lines (not present in the original figure). The triadic grouping shown (whatever its actual form) is clearly vestigial, since it is absent in adult forms. The pore-pairs seem in process of becoming single by loss of the outer member.

The Origin of Flint.

By R. M. BRYDONE, F.G.S.

MR. W. A. RICHARDSON'S paper in the December, 1919, number of this Magazine has furnished a very useful summary of the problem of the origin of flint, with some very interesting suggestions; but it cannot be allowed to pass altogether unchallenged.

It is a pity that he did not attempt to clear up the confused terminology of Chalk flint. There are, broadly, three kinds: separate flints in rows, interstratified continuous lines of flint, and contrastratified continuous lines of flint. Such terms as lines, bands, seams, layers, beds have been used indiscriminately of all three kinds. It is very desirable that some distinctive term such as "vein" should be attached to the third class, the continuous flint which at any part of its course breaks across the stratification; while "tabular" might be restricted to the interstratified continuous flint, and "row", a term which cannot suggest either vein or tabular flint, employed for lines of separate flints.

The paper is vitiated by the basic but very dubious assumption that all Chalk flint must have originated at the same time. Is it, in fact, conceivable that the interstratified rows of hollow flints can be all contemporaneous with the veins? These hollow flints practically always contain some amount of soft, loose powder, with an abnormal proportion of fossils in exceptional preservation, and a large majority have a loose spongiform nucleus. The formation and preservation of this assemblage seem to be